

MIOCENE FOSSIL GRASSES: POSSIBLE ADAPTATION IN REPRODUCTIVE BRACTS (LEMMA AND PALEA)¹

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ABSTRACT

Fossil reproductive bracts of *Berriochloa*, *Nassella*, and *Paleoeriocoma* of the tribe Stipeae, *Archaeoleersia* of the tribe Oryzeae, and *Panicum* of the tribe Paniceae (Gramineae) were collected from late Oligocene–Miocene strata in central North America, examined, and compared with modern taxa. One objective of these studies was to elucidate the evolution and possible adaptive significance of bract features. *Berriochloa*, the oldest known grass, appears in late Oligocene–early Miocene strata, where it has an indurate, cylindrical anthoecium (lemma and palea collectively) and an elongated, pointed callus. From early Miocene forms of *Berriochloa* two mid-late Miocene lineages evolved, one retaining a cylindrical anthoecium and the other developing a prominently inflated anthoecium. Both lineages retained the elongated, pointed callus. *Paleoeriocoma*, *Nassella*, *Archaeoleersia*, and *Panicum* first appear in the late Miocene with anthoecia similar to those of living taxa. The indurate anthoecium of the fossil and related living grasses probably evolved primarily as an adaptation to mammals and insects that use grasses as food. Related living taxa show adaptive mechanisms similar to those of the fossils, although some features such as the strongly interlocking bracts and blunt callus of some species of *Piptochaetium* are a post Miocene development.

The Tertiary deposits of central North American Plains have produced rich and varied floras of considerable paleobotanical interest (Stansbury, 1852; Engelman, 1876; Cockerell, 1914; Berry, 1928; Elias, 1931, 1932, 1934, 1935, 1942; Frye et al., 1956, 1978; Leonard, 1958; Leonard & Frye, 1978; Frye & Leonard, 1959; Segal, 1965, 1966a, 1966b, 1966c; Skinner et al., 1968; Galbreath, 1974; Diffendal et al., 1982; Voorhies & Thomasson, 1979). Grasses in these floras are found as silicified reproductive bracts or as remains of leaves, stems, and roots and frequently exhibit detailed epidermal features that aid in determining phylogenetic relationships of fossils and their modern counterparts (Thomasson, 1976, 1977, 1978, 1979, 1980a, 1980b, 1984). Fossils described include reproductive bracts assigned to *Archaeoleersia* of the tribe Oryzeae, *Berriochloa*, *Nassella*, and *Paleoeriocoma* of the tribe Stipeae, and *Panicum* of the tribe Paniceae and leaf fragments assigned to the subfamilies Festucoideae and Arundinoideae.

This paper presents results of my studies of the reproductive bracts (lemma and palea) or bract (lemma) enclosing the mature grain or caryopsis of fossil grasses and their related living taxa. It reviews the geologic and paleoecologic back-

ground, summarizes the morphologic features of the fossil and living grasses, examines evolutionary trends among the fossil grasses, and speculates on the adaptive significance of features seen in fossil and living grasses.

GEOLOGIC AND PALEOECOLOGIC BACKGROUND

The late Tertiary (Oligocene–Pliocene) strata of the central part of North America are a widespread group of continental sediments extending from North Dakota and Wyoming to Texas and New Mexico that were deposited principally in fluvial and aeolian environments. They consist of a large variety of sediments including clays, silts, sands, conglomerates, freshwater diatomites, and volcanic ashes and vary in thickness in individual sections from more than 200 m to 1 m. Although some early studies suggested rather simple models of deposition and biostratigraphy, more recent investigations have demonstrated their depositional and biostratigraphic complexity (Bart, 1975; Breyer, 1976, 1981; Skinner et al., 1968, 1977; Swinehart, 1979; Thomasson, 1979; Diffendal, 1980, 1982). Among the most richly fossiliferous Tertiary strata in the world, they contain assemblages of

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TABLE 1. Stratigraphic relationships and ages of late Tertiary strata and study sites in the plains of central North America.

Epoch (Ma)	North American Land Mammal Age (Ma)	Study Sites ^a	Formation
Pliocene — 5 —	Blancan — 4.5 —		
	Hemphillian — 9 —	85	Ogallala
	Clarendonian — 11 —	9, 50, 56	
Miocene	Barstovian — 16 —	56	
	Hemingfordian — 20 —	64, 65	Sheep Creek
		79, 81	Harrison–Monroe Creek
	Oligocene — 24 —	Arikareean	

^a Geographic localities: Kansas, west-central (9); Nebraska, west-central (50, 79), northeastern (56), northwestern (64, 65); Texas, northern (85).

fossil plants and animals that have been the subject of numerous taxonomic and biostratigraphic studies for nearly 150 years. Some of the most paleontologically productive of these deposits are, from the oldest to the youngest, the Harrison, Sheep Creek, and Ogallala (including the Valentine, Ash Hollow, and Kimball) Formations. The geographic locations of several major study sites, the general stratigraphic relationships, and ages of the geologic formations and the stratigraphic levels from which fossil grasses have been studied are shown in Table 1. The stratigraphy, biostratigraphy, and lithologic characteristics of each of these formations have been studied extensively, and the reader is referred to these studies for further information (Harrison–Yatkola, 1978; Swinehart, 1979; Sheep Creek—Skinner et al., 1977; Ogallala—Breyer, 1976, 1981; Thomasson, 1979; Swinehart, 1979; Diffendal, 1982). An excellent historical review of the various interpretations of the stratigraphic relationships of these formations is that by Galusha (1975).

The vertebrate faunas found in each of the formations include abundant grazing and semi-grazing cursorial animals such as camels, horses, and rhinoceroses. This suggests savanna or savanna parkland was present in the central plains of North America throughout the late Oligocene and Miocene. Based on the abundance of aeolian

sediments in the late Oligocene and early Miocene strata, the environment during this period appears to have been arid to semi-arid (Swinehart, 1979). However, by the middle and late Miocene the environment was more humid and probably subtropical, as indicated by the preponderance of sediments deposited by fluvial processes and by the presence of vertebrates such as large land tortoises and crocodiles in the strata (Holman, 1971; Voorhies, 1971; Thomasson, 1979). The abundance of volcanic ash in the sediments indicates widespread and massive volcanic activity during deposition of all of the formations (Skinner et al., 1977; Yatkola, 1978; Thomasson, 1979; Swinehart, 1979; Voorhies, 1981), but the climatological and perhaps evolutionary effects of this activity have not been explored. Fossil wood with annual rings suggests that wet and dry seasons were probably present throughout the period from the late Oligocene to late Miocene, but the extremes of winter and summer present on the plains today are probably a post Miocene development.

FEATURES OF GRASS ANTHOECIA

In order to reasonably speculate about the adaptive significance of features seen on the bracts of fossil and living grasses it is necessary to re-

TABLE 2. Husk features of Late Tertiary fossil grasses and related living taxa. Explanation of symbols: * = fossil genus; c = obconic, d = cylindrical, f = fusiform, k = biconvex, l = lenticular, n = oblong, s = spheroid, v = obovate; o = absent, + = present; b = blunt, s = sharp; a = papillae, h = hooks, i = microhairs, m = macrohairs, t = "pointless" hooks, p = prickles.

Genus	Shape	Interlocking Lemma and Palea	Callus Type	Surface Structures of the Lemma	Silica Bodies on the Lemma
<i>Berriochloa</i> *	c, d, n, s, v	o	s	h, m, p	o
<i>Piptochaetium</i>	c, d, n, s, v	+	b, s	h, m, p, t	o
<i>Stipa</i>	d, n	o	s	h, i, m, p	o, +
<i>Nassella</i> *	f, v	o	b	h, m	o
<i>Nassella</i>	f, l	o	b	h	o
<i>Paleoeriocoma</i> *	f	o	b	h, m	o
<i>Oryzopsis</i>	f, n	o	b, s	h, i, m, p	o, +
<i>Panicum</i> *	k	o	b	a	o
<i>Panicum</i>	k	o	b	a	o
<i>Archaeoleersia</i> *	l	+	b	a, i, p	o
<i>Leersia</i>	l	+	b	a, i, p	+

view the nature and occurrence of the features. Only those taxa represented by both living and related fossil forms will be considered, although discussions of the features are undoubtedly relevant to many other taxa. Summaries of the features of the fossil grasses and their related living counterparts are given in Tables 2 and 3.

SHAPES OF THE ANTHOECIUM

In living grasses the shape of the mature anthoecium is extremely variable, being narrowly to broadly cylindrical or oblong in *Stipa* and some *Piptochaetium*; spindle-shaped, obovate, oblong, or nearly spheroid in *Oryzopsis*, *Piptochaetium*, and *Nassella*; biconvex in *Panicum*, and lenticular in *Leersia* and some *Nassella*. In early studies the anthoecium shape was thought to be generically distinct, but as Barkworth (1983a, 1983b) and I (Thomasson, 1976, 1979, 1980b) have shown, this is not true. For example, in the genus *Piptochaetium* the shape of the anthoecium varies from elongate, cylindrical in *P. avenaceum* (formerly *Stipa avenaceum*), to obconic in *P. uruguense*, to spheroid in *P. stipoides*. Further, I have suggested that taxa such as *S. viridula* and *S. robusta*, which have been assigned to the genus *Stipa* on the basis of their oblong to cylindrical anthoecia with pointed calli, probably belong in the genus *Oryzopsis* on the basis of micromorphological features (Thomasson, 1981). More studies such as the one conducted by Barkworth (1983b) are needed to determine accurately generic relationships and limits in the Stipeae.

Anthoecium shapes found among the fossil grasses are similar to those found in living forms. Although *Stipa* and *Piptochaetium* are not found as fossils, their common ancestor *Berriochloa* is present and varies in shape from cylindrical to spheroid (Parodi, 1944). Similarly the living grasses *Oryzopsis* and *Leersia* are represented in the fossil record by *Paleoeriocoma* and *Archaeoleersia* respectively, and the shapes are nearly identical (Thomasson, 1980a, 1980b).

TYPES OF CALLI

The callus in grasses is an extension of the anthoecium below the base of the lemma and palea. Generally it is an extension of the lemma, and it may be elongate to short and sharply pointed or blunt (Figs. 1, 2). Commonly the sharply pointed type is associated with an elongate, cylindrical or oblong anthoecium and the blunt type with a more robust, obovate or spheroid shape. Grasses assigned to *Stipa* usually have pointed calli whereas those assigned to *Oryzopsis* and *Nassella* have short, slightly pointed to blunt calli. *Piptochaetium* is the most variable with respect to the callus: elongate and sharply pointed in *Piptochaetium avenaceum* and short and blunt in *P. stipoides* and *P. montevidense*.

The various types of callus found in living grasses were also found in fossil grasses, but their distribution among fossils sometimes differs from that in living grasses. Thus, while calli found on species of fossil *Paleoeriocoma* and *Nassella* were similar to those on species in related, living *Oryzopsis* and *Nassella*, all species of *Berriochloa*, regardless of the shape of the anthoecium, have

TABLE 3. Features of the husks of Miocene fossil grass genera and related living genera of the tribe Stipeae. Explanation of symbols: * = fossil; ** = Thomasson, 1978; o = absent; a = well developed and indurate; b = moderately or weakly developed and not indurate; c = well developed and prominent; d = moderately or weakly developed.

Genus	Palea	Grooved Palea	Raised Lateral Walls on Long Cells**	Spheroid Husks	Long Cells Several Times Longer than Wide	Sharp Callus
<i>Berriochloa</i> *	a	o	o	c	c	c
<i>Piptochaetium</i>	a	c	c	c	o, c	o, c
<i>Stipa</i>	a, b	o	o	o	o, c	c, d
<i>Nassella</i> *	o	o	o	o	o	o
<i>Nassella</i>	o, b	o	o	o	o	o
<i>Oryzopsis</i>	a	o	o	o	o, c, d	o
<i>Paleoeriocoma</i> *	a	o	o	o	d	o

sharply pointed calli. This suggests that the evolution of the blunt callus as found in several species of *Piptochaetium* is a post Miocene event.

INDURATION OF THE BRACTS

In all of the living genera considered during this study, the lemma at maturity was indurate, but the palea was equally indurate in *Leersia*, *Oryzopsis*, *Panicum*, *Piptochaetium*, and *Stipa*, membranaceous in some *Stipa* and rarely some *Nassella*, and absent in most *Nassella*. In any case, at maturity the lemma and palea or lemma alone form a rigid container that encloses the ripe caryopsis (Fig. 3).

Among the fossils, the lemma and palea were well developed and apparently indurate (as judged by the preservation of the bracts) in all taxa except *Nassella*, in which the palea was absent.

INTERRELATIONSHIP OF THE LEMMA AND PALEA

At maturity the lemma and palea or lemma alone form a container for the caryopsis, but this happens in several different ways depending on the interrelationship of the lemma and palea. In species of *Stipa* and *Nassella* with an indurate lemma and a membranaceous palea or no palea at all, the lemma wraps around on itself and forms the rigid anthoecium. In other taxa in which both the lemma and palea are indurate and play a role in the development of the anthoecium, two conditions may occur. First, as in many

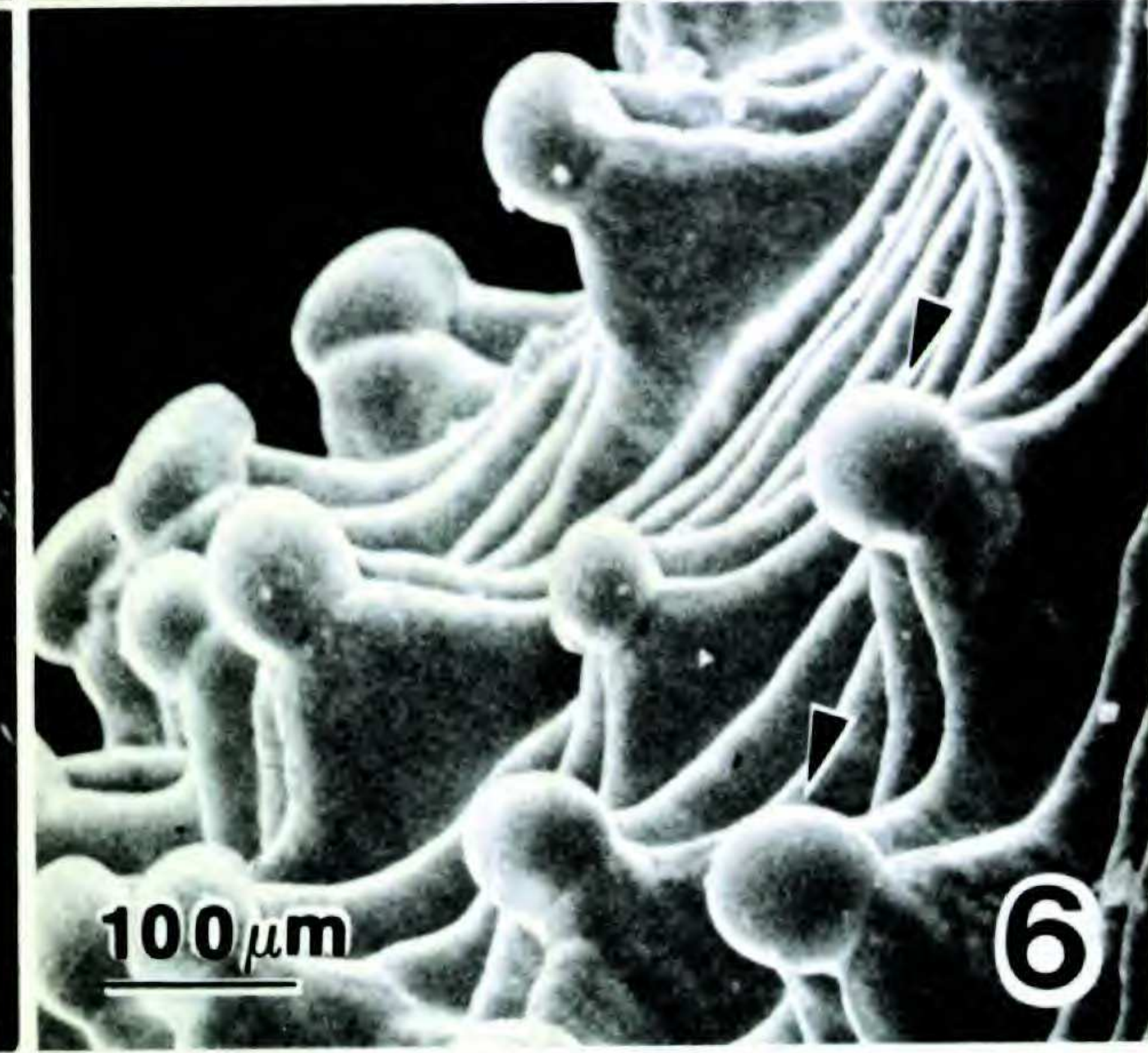
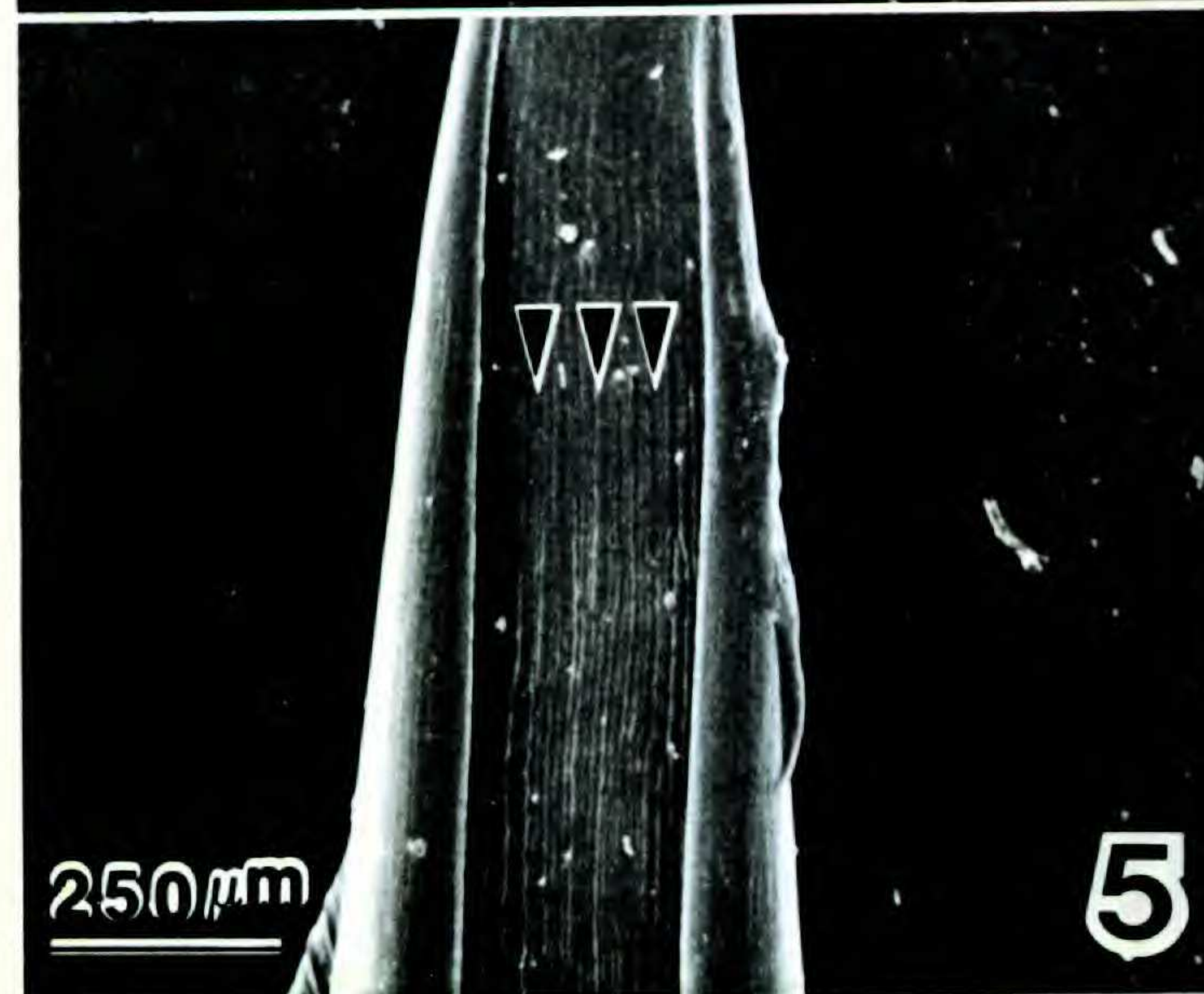
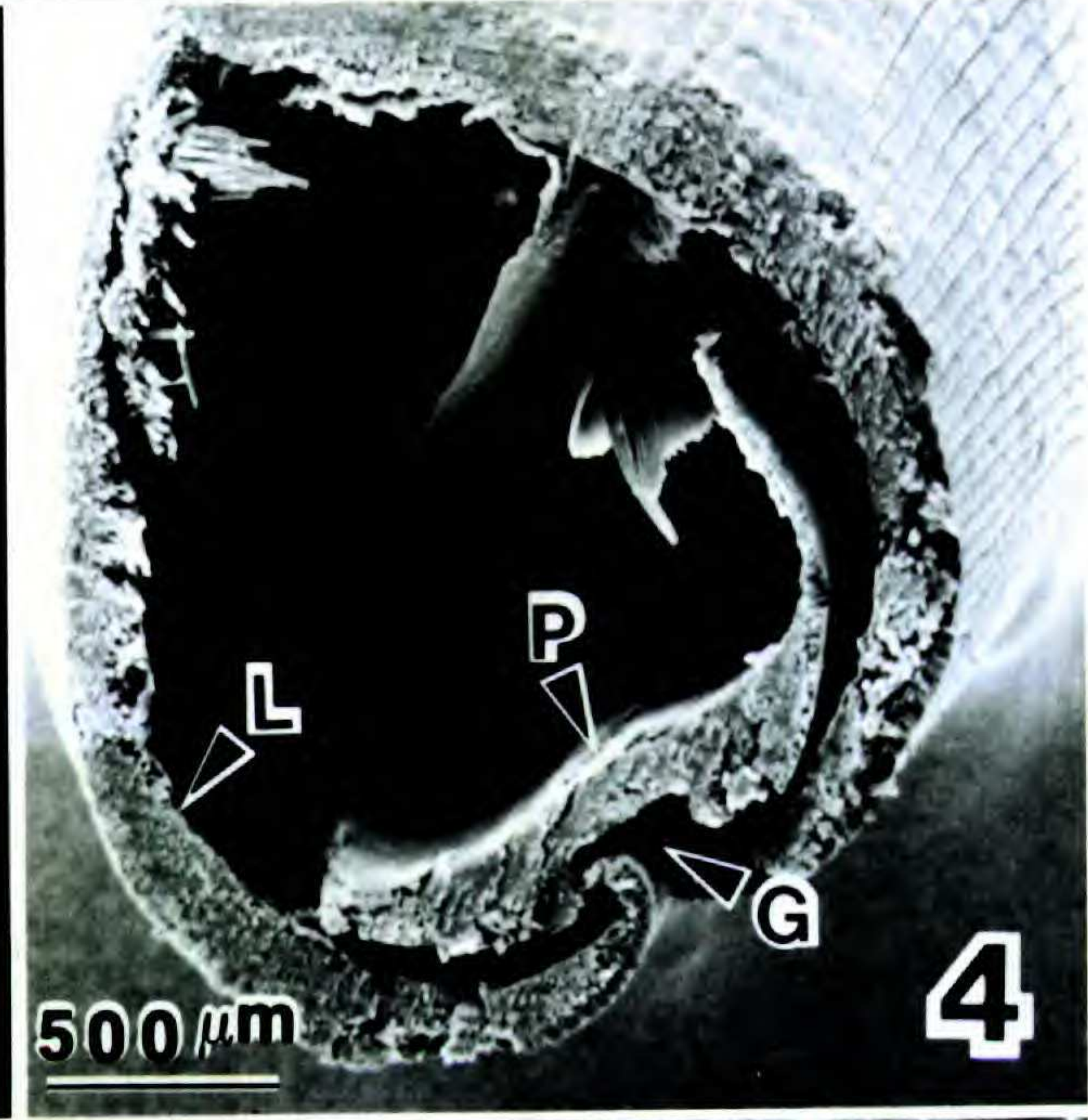
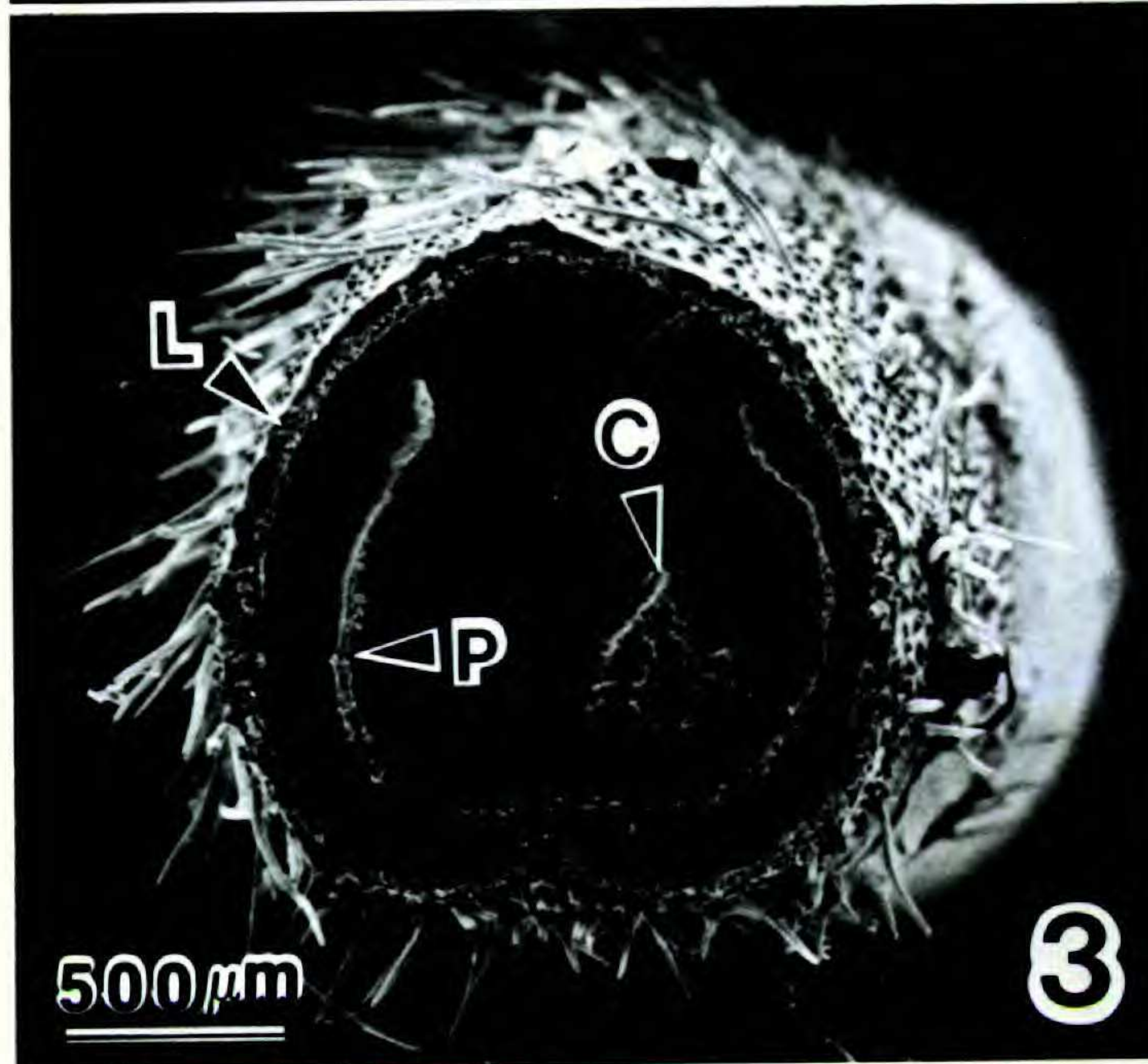
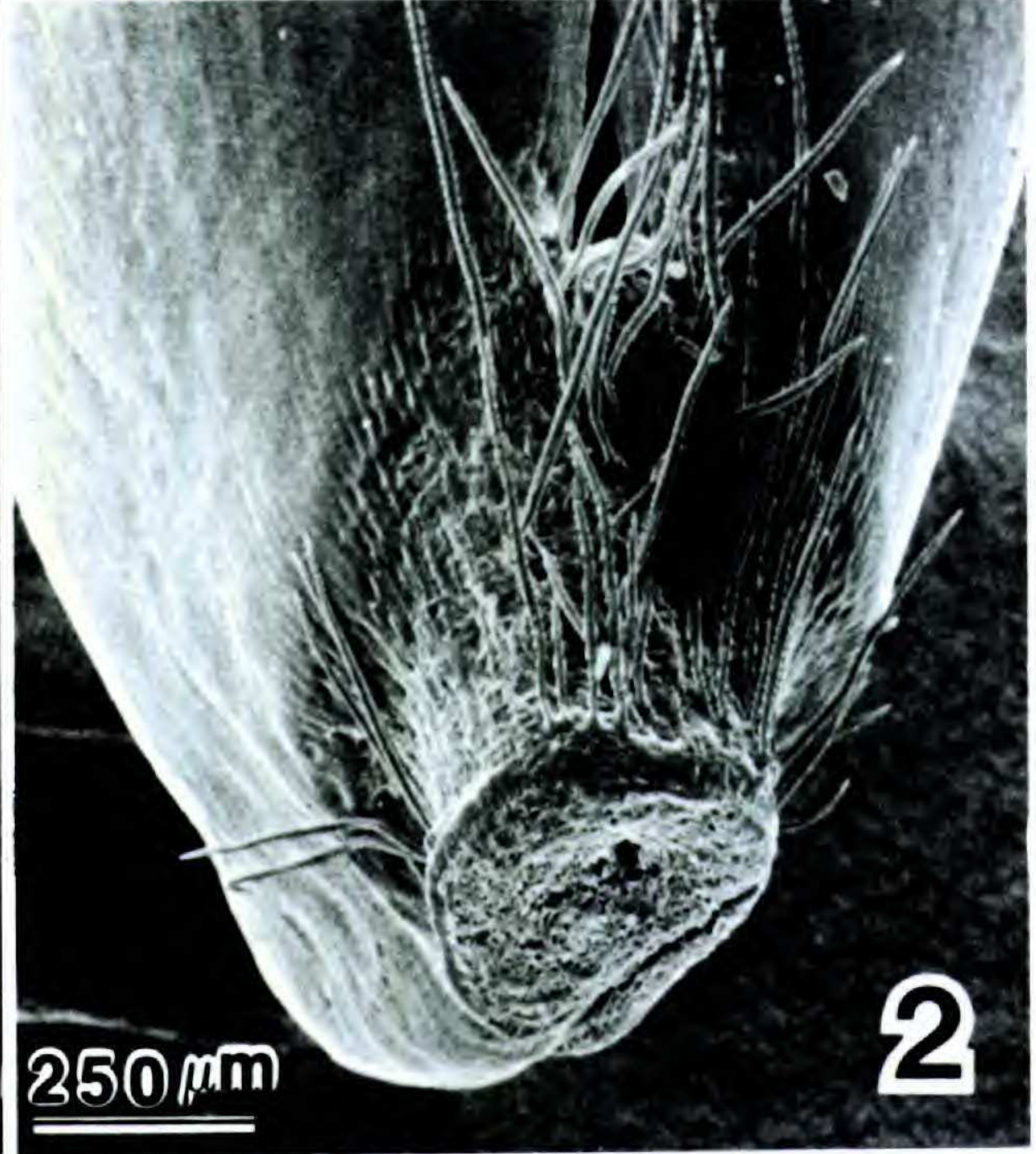
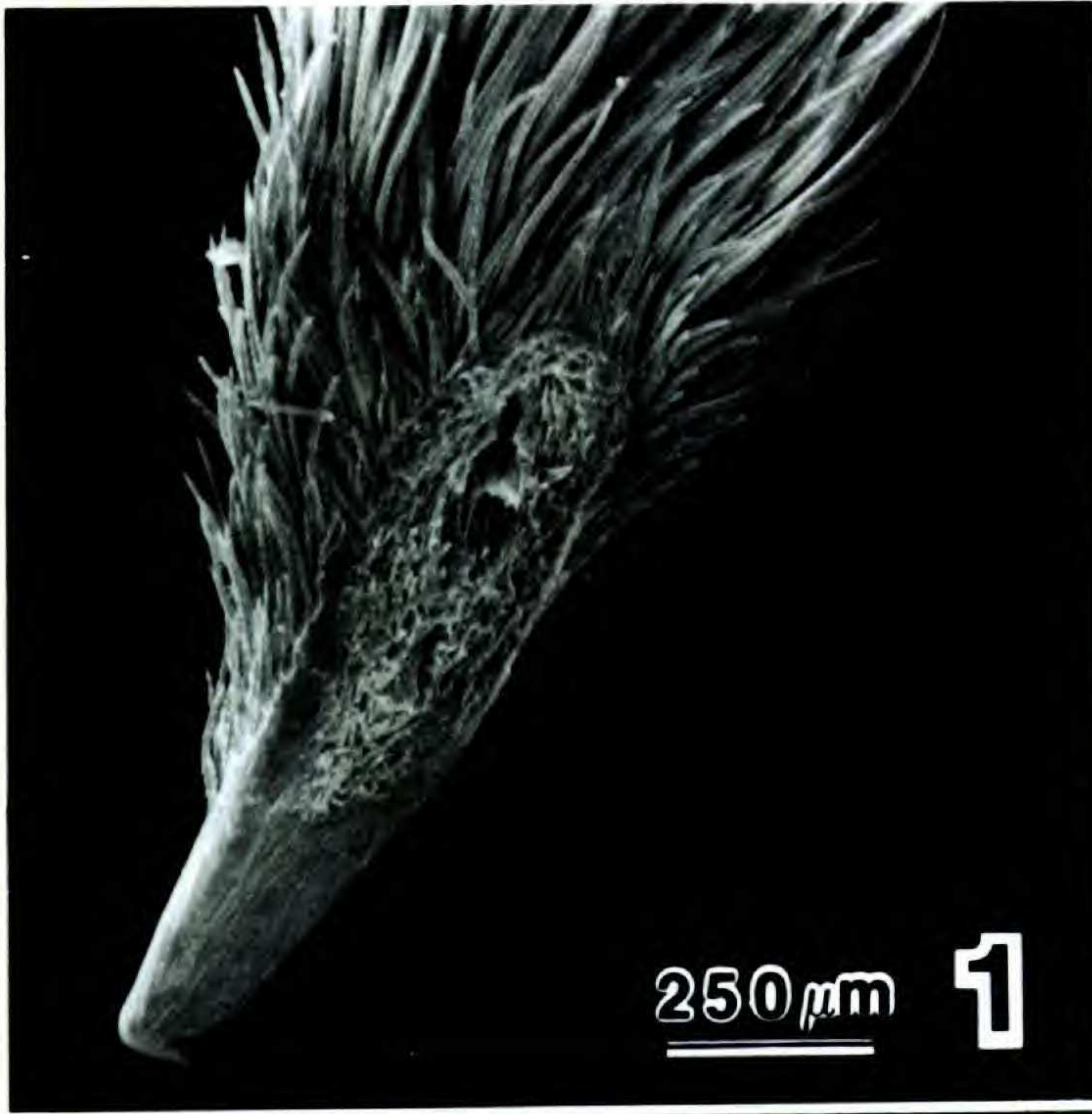
species of *Stipa* and *Oryzopsis*, the two bracts may simply overlap with the lemma externally, thereby forming the anthoecium (Fig. 3). In the second condition the rigid anthoecium is formed by the physical interlocking of the lemma and palea as in *Leersia*, *Panicum*, and *Piptochaetium* (Figs. 4, 5). The lemma and palea may be weakly interlocked as in *Panicum* or strongly so as in *Leersia* and *Piptochaetium* in which the lemma interlocks into prominent grooves of the palea (Thomasson, 1976, 1980a).

The interrelationship of fossil lemma and palea is the same as in living taxa except the grooved palea of *Piptochaetium* is absent in *Berriochloa* so that this feature apparently evolved after the Miocene. The strongly grooved and interlocked palea found in *Leersia* is present in the related Miocene *Archaeoleersia*.

MICROMORPHOLOGICAL STRUCTURES OF THE LEMMA AND PALEA

Types of micromorphological structures found on lemmas and paleas of living taxa investigated include macrohairs, prickles, hooks (= barbs, crochet, or crown cells), papillae, silica bodies, and microhairs (see Metcalfe, 1960; Ellis, 1979; or Palmer and Tucker, 1981, 1983 for detailed descriptions of the different types of structures). One interesting variation of these structures is a type of hook found on *Piptochaetium montevidense* in which the point at the apex of the hook

FIGURES 1-6.—1. Elongate, pointed callus of *Piptochaetium avenaceum*.—2. Blunt callus of *Piptochaetium brevicalyx*.—3. Cross section of the mature anthoecium of *Stipa comata* with enclosed caryopsis (C). Note the overlapping relationship of the lemma (L) and palea (P).—4. Cross section of the anthoecium of *Piptochaetium*



bicolor. Observe that the lemma (L) interlocks with the palea (P) in a palea groove (G).—5. Palea removed from the anthoecium of *Piptochaetium avenaceoides* to show distinct medial groove (arrows).—6. Lemma surface of *Piptochaetium montevidense* showing “pointless” hooks (arrows).

is greatly reduced or entirely absent (Fig. 6). While I refer to these structures as "pointless" hooks, I speculate later that, in combination with the anthoecium shape, they actually have an important function in protecting the caryopsis. Except for "pointless" hooks, all surface structures observed on living taxa were also observed on fossil taxa.

EVOLUTIONARY TRENDS IN FEATURES OF THE GRASS ANTHOECIUM

One of the most obvious trends that I and others (Elias, 1942) have observed in fossil grasses is the change in anthoecium shape in the genus *Berriochloa*. The oldest known late Oligocene–early Miocene fossil grasses [Harrison–Monroe Creek (undifferentiated) Formation, 23 Ma] have anthoecia that are elongate cylindrical (e.g., *B. schereri*). These are succeeded in the middle Miocene (Sheep Creek Formation, 17 Ma) primarily by grasses such as *Berriochloa minima*, that have elongate cylindrical anthoecia, although at least two grasses (*B. primaeva* and *B. dawesense*) from this period have more inflated, oblong anthoecia. By the late Miocene (Ogallala Formation, 8–12 Ma) two lines of grasses emerge based on the shape of the anthoecia. In one line (e.g., *Berriochloa communis* and *B. grandis*) the anthoecium is elongate and cylindrical whereas in the second (e.g., *B. glabra* and *B. inflata*) the anthoecium is inflated and obconic to nearly spheroid.

A second trend among fossil grasses is an increase in overall size of the anthoecia in the genus *Berriochloa*. Species found in older strata of the Harrison and Sheep Creek Formations (e.g., *Berriochloa schereri* and *B. minima*) have anthoecia that are predominantly cylindrical to oblong and small (length 1.5–5 mm and width 0.4–1.4 mm), whereas in much younger strata of the Ogallala Formation species (e.g., *B. grandis* and *B. communis*) with similarly shaped, but larger anthoecia (length 3–12 mm and width 0.7–2.5 mm) are common. Likewise, the only species with inflated, obovate to fusiform anthoecia that occur in older strata (*Berriochloa primaeva* and *B. dawesense* in the Sheep Creek Formation) have small anthoecia (length 1.1–4.5 mm and width 0.6–1.4 mm), whereas there are several species (e.g., *B. maxima*, *B. glabra*, *B. tuberculata*, and others) with very robust, fusiform to spheroid anthoecia (length 2.5–8 mm and width 2.2–3.5 mm) that

are found only in the much younger Ogallala Formation.

A final trend among the fossil grasses is an increasing variety of taxa from older to younger strata. This is true even though thousands of specimens from each stratigraphic level are known. In the oldest levels only the genus *Berriochloa* is known and is represented by two species, whereas in the younger strata of the Sheep Creek Formation as many as seven species of *Berriochloa* are known. In the late Miocene Ogallala Formation an explosion in the numbers of taxa of fossil grasses occurs, with as many as 20 species of *Berriochloa* being known, in addition to species of *Archaeoleersia*, *Nassella*, *Panicum*, and *Paleoeriocoma*.

Although exact explanations for the trends among fossil grasses are unknown, it is possible to speculate on their causes and adaptive significance.

I believe that evolution of the two lines of anthoecium shapes (elongate, cylindrical and inflated, fusiform to spheroid) appears primarily to represent a response to the coevolution of grasses with animals and insects that ate the caryopsis as food (see section later in this paper on the adaptive significances of anthoecium features). This suggests that the shape of the anthoecium has limited taxonomic utility (i.e., unrelated taxa may have similarly shaped anthoecia), and this finding has been supported by my studies, at least at the generic level. To illustrate, when the first fossil grasses of the tribe Stipeae were recovered from the High Plains Tertiary strata two taxa, *Stipidium* and *Berriochloa*, were described primarily on the basis of the anthoecium shape, the former having cylindrical anthoecia and the latter having inflated anthoecia (Elias, 1932). However, I have since shown that anthoecium shape alone cannot be used in determining generic relationships in the fossil and modern Stipeae, but rather that a combination of micromorphological and macromorphological features of the anthoecium must be used (Thomasson, 1979, 1981) (Table 3).

I speculate that increasing size of anthoecia is a long term response to foraging insects such as harvester ants. It is well known that these insects collect large numbers of grass anthoecia (Wheeler & Wheeler, 1963; Davison, 1982), and that they select seeds according to size (i.e., the smaller the body length of the forager the smaller the seeds collected) (Davison, 1982). An increasingly larger anthoecium might have reduced foraging on

the caryopsis of species with large anthoecia and thus favored those species with increased survival of caryopses, each of which could potentially germinate and produce a new plant.

Finally, with respect to the increasing variety of taxa, several explanations are possible including increased immigration of new taxa, more complex environments with more diverse ecological niches, or more favorable conditions for preservation (e.g., more alkaline groundwaters resulting in more silica in solution). In the genus *Berriochloa* the increasing variety of species might reflect increasingly diverse responses of grasses to their coevolution with foraging animals and insects.

ADAPTIVE SIGNIFICANCE OF ANTHOECIUM FEATURES

An important goal of my studies of Tertiary grasses and their living counterparts has been to discern the adaptive significance of the anthoecium features. Based on my studies and observations and those of others, it is possible to speculate on the adaptive significance of grass anthoecium features:

1. *Rigid indurate anthoecium*.
 - a) Protection from damage to the caryopsis during ingestion by mammals. Evidence from recent and fossil fecal deposits and from anthoecia associated with skeletal remains (Parodi, 1944; Voorhies, 1974; Thomasson, 1976; Voorhies & Thomasson, 1979).
 - b) Protection from insects that feed the caryopsis to larvae. Evidence from both modern and fossil burrows (Wheeler & Wheeler, 1963; Davison, 1982; Thomasson, 1982).
2. *Pointed callus*.
 - a) Aids in dispersal of anthoecium with enclosed caryopsis through attachment to the hide or entanglement in the hair of mammals (Parodi, 1944; unpubl. data).
 - b) Burial of the anthoecium and caryopsis in the soil (Barkworth, 1983a; unpubl. data).
3. *Blunt callus*. The absence of a sharply pointed callus may facilitate rapid movement of the anthoecium through the digestive tracts of mammals.
4. *Cylindrical anthoecium*. The narrow, elongate anthoecium facilitates burial in cracks in the soil (Barkworth, 1983a; unpubl. data).
5. *Inflated anthoecium*.
 - a) In combination with the blunt callus, the inflated shape allows for more rapid movement of the anthoecium through the digestive tracks of mammals (Parodi, 1944).
 - b) The inflated shape protects against use by many insects that have great difficulty in moving all other similarly shaped disseminules (Davison, 1982).
6. *Surface structures*.
 - a) Pointed surface structures such as hooks may aid in the entanglement of the anthoecium in the hair of animals.
 - b) Large pointed features such as macrohairs, especially on the callus, aid in the burial of the anthoecium by making it difficult for the anthoecium to come free once lodged in cracks in the soil (Barkworth, 1983a; unpubl. data).
 - c) Blunt, raised structures such as papillae and "pointless" hooks, especially in combination with inflated anthoecia with blunt calli, facilitate rapid movement of the anthoecium through the digestive tracts of mammals.
7. *Grooved palea*. May act as a mechanism to securely lock the lemma and palea together for increased protection of the caryopsis during passage of the anthoecium through the digestive tracts of mammals.

The degree to which anthoecium features are interrelated is particularly interesting. For example, the anthoecium of the South American grass *Piptochaetium montevidense* has a combination of features that include an indurate, obovate anthoecium formed by a strongly interlocking lemma and palea, a short, blunt callus, a lemma surface covered with large "pointless" hooks, and a readily deciduous awn. Rather than asking what the function of any single feature is, the question that I think must be answered is: What is the function of the combination of characteristics observed? For example, common sense suggests that the rigid, indurate anthoecium probably functions in protecting the caryopsis from something. But from what? In order to answer that question and others concerning the adaptive significance of anthoecium features, I have examined evidences from both the past and present, and I have concluded that the principal factor acting on the evolution of many of the features seen on the fossil and living grasses is the co-

evolution of the grasses with animals and insects that ingest (purposely or inadvertently) the caryopsis. In arriving at this conclusion all of the features of the anthoecium have been considered. Thus, in the case of *P. montevidense* the features observed should protect the caryopsis by aiding the rapid movement of the anthoecium through an animal's digestive tract (rounded shape, rough surface, and blunt callus) while preventing damage by digestive juices (indurate, interlocking bracts). Features seen on a grass such as *Stipa comata*, however, would allow for easy burial of the anthoecia in cracks in the soil (cylindrical anthoecium with a hairy, sharp callus and persistent awn) while providing protection to the caryopsis from foraging insects and mammals (indurate, overlapping bracts). Although factors of the environment such as mesic and xeric habitats probably have influenced the evolution of certain features of the anthoecium (e.g., the sharp callus) the features have not been influenced to the degree suggested by Barkworth (1983a).

CONCLUSION

Many features of grasses that have allowed them to be phenomenally successful in competition with other plants, animals, and insects have a long geologic history. The results of my studies of fossil and living grasses have suggested possible explanations of the adaptive significance of many features of grass anthoecia and have provided a better understanding of the evolution of grasses. Whereas most of the fossil history of grasses and the actual origins of many grass features are unknown, the widespread distribution of Cretaceous and Tertiary deposits containing abundant floras provide unlimited opportunities for future exploratory studies on the intriguing question of grass evolution.

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